

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3216, 14 pp., 4 figures, 2 tables
December 31, 1997

A Reappraisal of Trigoniacean Families (Bivalvia) and a Description of Two New Early Triassic Species

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ABSTRACT

Our 1975 proposal that the complex trigonian dentition was independently acquired by three separate but related families assumed that external morphology was more stable than hinge structure during evolution of the Trigoniacea. This hypothesis is not supported by our further work and the experience of other workers, so we have reinterpreted the Schizodidae, Myophoriidae, and Trigoniidae emphasizing hinge grades as family characteristics.

The myophorian grade is distinguished by myophorous buttresses and a posterior wing on tooth 2, both lacking in the schizodian hinge. Tooth striation is either absent or sporadically developed.

By contrast, the tight-fitting teeth and sockets of the strongly buttressed trigonian hinge interlock along conspicuously striated faces, and tooth 2 is broad and biramous.

In returning to the conventional distinction between Myophoriidae and Trigoniidae, we abandon Costatoriidae and demote Eoastartidae to a subfamily of Schizodidae.

Two additions to the sparse Early Triassic record of the Trigoniacea, *Neoschizodus elongatus* n. sp. and *Lyriomyophoria paullorum* n. sp., are described from the Spathian Virgin Limestone of southern Nevada. The hinges of these new species represent a transitional state between myophorian and trigonian grades.

INTRODUCTION

Love the organisms for themselves first, then strain for general explanations, and, with good fortune, discoveries will follow. If they don't, the love and the pleasure will have been enough.

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Two decades have passed since we proposed a classification of the Trigoniacea based on the hypothesis that shell ornamentation is more important than hinge morphology for recognizing the main lines of phyletic divergence in the superfamily (Newell and Boyd, 1975). Our subsequent appraisal of this concept results in a different conclusion.

We had thought that the distinctive trigonian dentition was independently acquired by three separate but related lineages. These three, the mainly unornamented Myophoriidae, the annulate Trigoniidae, and the radially ribbed Costatoriidae, branched from the ancestral line (Schizodidae) early in the Permian Period. In each branch, the primitive hinge condition (schizodian grade) underwent similar modifications recognized successively as myophorian and trigonian grades.

This interpretation of parallel hinge evolution in several families was a striking departure from the concept employed in the Treatise on Invertebrate Paleontology (Cox, 1969). There, most trigoniaceans with schizodian and myophorian hinges are grouped in the family Myophoriidae (Paleozoic and early Mesozoic) and numerous younger genera with trigonian hinges constitute the family Trigoniidae, conventionally thought to be monophyletic.

Since 1975, several important papers, especially Fleming (1987), on post-Paleozoic trigoniaceans have disagreed with our 1975 phylogenetic hypothesis. It is not supported by the experience of these authors, so we revert to the traditional emphasis on hinge grade as a family characteristic.

Here we discuss the trigonian hinge grade, and reappraise our families, describing two new species that supplement the sparse Lower Triassic trigoniacean record.

THE THREE TRIGONIACEAN HINGE GRADES

The typical schizodian hinge, present in most Paleozoic trigoniaceans, consists of two teeth, one major and one minor, on each valve. The teeth are not striated and a myophorous buttress is absent.

Undoubted pre-Carboniferous examples

are rare, and we have nothing to add to our previous discussion of the Devonian and Upper Silurian record (Newell and Boyd, 1975). Subsequent to that writing, Lower Silurian schizodian-like hinges were illustrated by Harrison and Harrison (1975: pl. 2, figs. 14–17). These tiny valves are juveniles of *Lyrodosma*, and several specialists have noted the possibility that late Paleozoic trigoniaceans evolved by neotenuous retention of this juvenile hinge (e.g., Pojeta et al., 1986).

The myophorian hinge, intermediate between schizodian and trigonian grades, possesses an anterior buttress, a third (posterior) tooth on the left valve, and a distinctive posterior elongation of that valve's major tooth. The elongation, a parallel-sided ridge, and the elongated posterior tooth of the right valve resemble the lateral teeth of heterodonts. Tooth striation is either absent or sporadically developed.

In the trigonian hinge, tight-fitting teeth and sockets interlock along conspicuously striated occluding faces. The central tooth of the left valve is broad and biramous, and the anterior end of the hinge is strengthened by a prominent buttress in each valve.

All three hinge grades include a parivincular ligament. Whereas the ligament, as evidenced by insertion groove and nymph, has varied only in length through trigoniacean history, trigonian dentition is the last in a chronologic sequence of hinge grades exhibited by the superfamily Trigoniacea.

THE TRIGONIAN HINGE

The trigonian hinge (fig. 1) is the distinguishing character of the important family Trigoniidae. In his diagnosis of this family, Poulton (1979: 14) provided a succinct description of the dentition:

Triangular tooth in left valve with ventrally diverging sockets on each side; sockets bear regular slightly curving striae. Subordinate elongate teeth anterior and posterior to the sockets. Two grooved teeth in right valve match the sockets of the left.

Two other characteristics of the trigonian hinge not specified in Poulton's statement are the bifid aspect of the triangular tooth on the left valve and a corresponding gap (hiatus) in the right-valve hinge plate. Johnston (1993: 107–111) discussed the functional

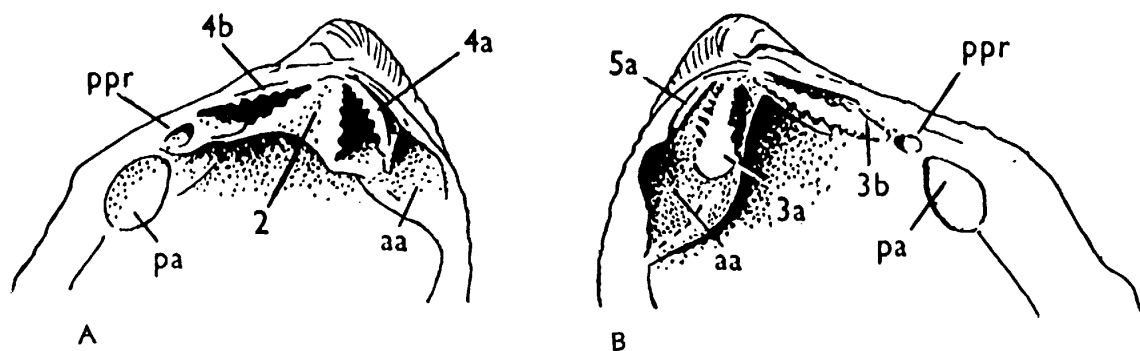


Fig. 1. *Trigonía* sp. Diagram of hinge notation used herein. A. LV; B. RV, modified from Cox, 1969: N472.

significance of this combination in allowing unobstructed passage of pedal elevator muscles from dorsal insertion points to an extended, trunklike foot.

It is clear from the literature on Mesozoic trigoniaceans that the terms "trigonian" and "trigoniid" are applied to a somewhat broader spectrum of hinges than that described by Poulton. The one feature implied by all workers who use these terms is the presence of tooth striation. The striae are parallel grooves on the anterior or posterior face of a tooth. Just as adjacent synclines and anticlines share a limb, so a given striated surface is shared by a socket and the adjacent tooth. Thus, some authors refer to striated sockets whereas others describe striated teeth. Although we prefer the term "striated" for this condition, various authors use "ridged," "grooved," or "secondary dentition" instead. These terms are easily misinterpreted since they are applicable to other aspects of tooth form.

Stanley (1978) provided a functional interpretation of tooth striation. Ubiquitous in trigoniids, the feature also typifies adult valves of the lower Paleozoic *Lyrodesma* (Cox, 1969) and occurs as an intraspecific variation in Permian *Astartella* (Boyd and Newell, 1968). Striated larval teeth are present in diverse living bivalve species (Waller, 1981: 46). This widespread taxonomic occurrence of a functional feature suggested to Waller (letter of April 15, 1997) the likelihood of its multiple origins in the Trigoniacea. Alternatively, he noted that absence of striation in adults of some trigoniacean

groups might be a derived pedomorphic feature.

We have not observed striae in Paleozoic representatives of the families discussed here, and we have found nothing in the literature to contradict our experience. Nakazawa (letter of July 9, 1996) did not observe striae in Japanese Permian species of *Neoschizodus* and *Costatoria*.

Striae are few and coarse in the earliest (Triassic) trigoniacean species to exhibit them (Newell and Boyd, 1975: 76), but they are numerous and regularly arranged in the typical trigonian hinge. Cox (1952: 46) called attention to the consistent asymmetry of individual ridges in an array of curved striae. The cross-sectional profile of any one ridge is gently sloping on the concave (dorsal) side and steeper, even slightly undercut, on the convex (ventral) side.

Poulton's description, quoted above, implies striation on the three left-valve teeth as well as on two prominent teeth of the right valve. This situation is illustrated in our figure 1. The figured hinge represents the maximum elaboration of the trigonian hinge grade, with three teeth and four striated faces in each valve. This condition is exemplified by the extant *Neotrigonia* and the Upper Cretaceous *Pteritrigonia* (*Scabrotrigonia*), although their minor teeth (4b and 5a) are inconspicuous.

We have argued on two occasions (Boyd and Newell, 1968; Newell and Boyd, 1975) against use of the Bernard system of hinge notation because of its implication of homology with specific aspects of the ontogeny

of heterodont bivalves. However, seeking the advantage of easy reference to particular teeth (not permitted by objective Steinmann notation) and recognizing that the Bernard scheme is well represented in trigoniacean literature, we employ the tooth designations of figure 1 in the subsequent discussion.

It is not surprising, given the common occurrence of mosaic evolution, that the various components of the trigonian hinge appear at different times in trigoniacean history. Many genera with hinges cited as trigoniid or trigonian don't possess all the features in figure 1, which leads to the question of the minimum requirements necessary for a hinge to be called trigonian. This has taxonomic importance if the trigonian condition is to be diagnostic for a family.

Incipient tooth striation, variable in degree and in location on the hinge, is present in several Triassic species (e.g., Newell and Boyd, 1975: 144). The literature on Mesozoic trigoniaceans contains numerous descriptions of taxa in which the hinge is designated as trigonian on the basis of less extensive tooth striation than that shown in figure 1. In describing the new Middle Triassic genus *Agonisca*, Fleming (1963) characterized the hinge as "fully trigoniid" but with "limited ridging on the teeth."

Early evidence of tooth striation in the trigoniacean record is found in *Neoschizodus thaynesianus* from the upper Lower Triassic of Utah (Newell and Boyd, 1975). In our collections of that species, some hinges lack striae whereas others have a few coarse striae on either the anterior face or both faces of tooth 2, and on complementary faces of right valves. We have found incipient striation of similar type in Middle Triassic species of *Gruenewaldia* and *Lyriomyophoria*.

The variable aspect of tooth striation in Triassic *Neoschizodus* has been observed by others. Fleming (1987: 18) characterized the genus as having "myophorian to trigonian" grade hinge, with the "sides of teeth and sockets smooth or transversely striated." He noted that Ichikawa (1954) erected *Okunometania* for *Neoschizodus*-like shells but with striated teeth, and that Farsan (1972) separated Afghanistan species of *Neoschizodus* into two subgenera based on presence or absence of striated teeth. Fleming stated that

New Zealand specimens of *Neoschizodus* cf. *N. laevigatus* show "a few coarse transverse striations" on tooth 2.

If the family Trigonidae is to be defined by dentition, Poulton's (1979) description of the trigonian hinge should be sharpened in two respects. First, regarding striation, we suggest that the minimum requirement for the trigonian hinge should be striae on both sides of tooth 2 and on both sides of tooth 3a. It follows that the opposing sockets will also be striated on both sides but, in this minimal condition, tooth 4b and its corresponding socket are smooth. Second, the posterior corner of the triangular tooth 2 should be at the convergence of two sloping surfaces, the ventral and posterior sides of the tooth. This excludes the parallel-sided posterior limb characteristic of the myophorian hinge.

The minimum requirements are met by some Triassic genera (e.g., Middle Triassic *Praegonia* and Upper Triassic *Maoritronia*) but not others (e.g., *Neoschizodus*; *Lyriomyophoria*; *Gruenewaldia*). Our admittedly limited knowledge of post-Triassic trigoniaceans suggests that they are typified by the trigonian hinge, although it is not adequately documented in many genera (e.g., Lower Jurassic *Liotronia*). At least one species with only minimal development of the trigonian hinge is present as high stratigraphically as Upper Cretaceous (e.g., *Yaadia hemphilli* as illustrated in Saul, 1978: pl. 10, fig. 6).

PROBLEMS WITH THE TAXONOMY OF NEWELL AND BOYD (1975)

Several specialists have raised serious objections to specific aspects of our 1975 family-level taxonomy for the Trigonacea. Criticism has centered on our revision of two families, Myophoriidae and Trigonidae, and our erection of the Costatoriidae. As Fleming (1987) pointed out, the last name is a junior synonym of Kobayashi's (1954) Minetrigoniinae. A more basic problem, however, involves our weighting of shell sculpture more heavily than dentition in family diagnoses.

COSTATORIIDAE

Our grouping of all trigoniaceans with radial ribs in the Costatoriidae resulted in a

family that ranges from Permian to Recent and includes representatives of the three major hinge grades known in the superfamily. Fleming (1987: 14, 24) granted the pragmatic advantage of radial ornament as a family character and utilized the Minetrigoniidae for radially ribbed Triassic trigoniaceans. However, he doubted the credibility of a lineage (our Costatoriidae) in which sculpture remained constant through several geologic periods while dentition changed.

The evolutionary continuity implied in our concept becomes suspect in light of the rarity of radial sculpture during the Jurassic-Cretaceous heyday of trigoniacean diversity, a fact emphasized by Saul (1978), Fleming (1987), and Cooper (1991). Fleming, noting the sporadic development of radial sculpture in early Cretaceous Australasian genera, thought it likely that the ornament originated independently in different lineages.

Regarding the radially ribbed *Neotrigonia*, Fleming (1987: 14) pointed out that the juvenile ornament suggests an ancestor with *Trigonia*-type sculpture rather than one with purely radial ornament. This supports his belief that the extant genus descended from *Eotrigonia*, not from older radially ornamented forms.

MYOPHORIIDAE AND TRIGONIIDAE

In a seminal paper, Cox (1952) distinguished between Myophoriidae and Trigoniidae on the basis of the hinge. For the latter, he emphasized the prominence of tooth 2, its conspicuous transverse ridges (striation), and the absence of a hinge plate between teeth 3a and 3b. This hiatus was thought to be absent in myophoriids. Striation was recognized in advanced myophoriids, but never to the conspicuous degree characteristic of trigoniids.

The two families have been widely adopted, together with the implication that the trigoniids are a monophyletic group descended from the Myophoriidae. Although Cox (1952: 48) had toyed with the idea of polyphyletic origin for the trigoniid hinge, his treatment of the superfamily in the *Treatise on Invertebrate Paleontology* ignored the topic and retained the two families as previously established.

Until our 1975 paper, no one had challenged Cox's view, and our alternative has not found support from experts on post-Paleozoic trigoniaceans (e.g., Poulton, 1979; Fleming, 1987; Cooper, 1991; Leanza, 1993). These specialists believe that the complex trigonian hinge is a conservative feature unlikely to have developed by parallel evolution in separate lineages. Although arguably true for the overall hinge, one aspect of the character complex described by Cox does seem to have developed independently at various times. The gap in the right valve hinge plate thought by Cox (1952) and Fleming (1964) to be a unique trigoniid feature is also found in some Paleozoic trigoniaceans of schizodian hinge grade (e.g., Newell and Boyd, 1975: fig. 12E; Johnston, 1993: fig. 78) and, less commonly, in myophoriids (e.g., Newell and Boyd, 1975: fig. 83C). While concluding that this hiatus evolved independently at different times, Fleming (1987: 12) reaffirmed its universality in the Trigoniidae and pointed out our mistake in labeling as a platform the umbonal mound beneath the hiatus in a photograph of *Neotrigonia* (Newell and Boyd, 1975, fig. 12A).

Our decision to recognize commarginal ornament as a diagnostic feature of the Trigoniidae represented a notable departure from the prevailing concept of that family. Annular shells comprising the Trigoniidae of our revision include representatives of all three hinge grades and the group ranges from Permian to Cretaceous. The argument noted above against independent origin of a trigonian-grade hinge is as applicable to the Trigoniidae as it is in regard to the Costatoriidae. However, our decision to abandon our hypothesis is also motivated by the ambiguous ornament of many taxa.

The Lower Jurassic *Liotrigonia* is described by Fleming (1987: 20) as having "purely concentric ornament" whereas Cox (1969: N473) characterized it as smooth "except for narrow, irregular subconcentric wrinkles mostly confined to anterior part." We (1975: 67) stated that it is "nearly smooth," and admitted our inability to tell whether that condition is primary or secondary.

Use of commarginal ornament as a criterion for family assignment becomes difficult

when shells combine two types of surface topography. Fleming (1987: 15) noted this problem in regard to Upper Triassic trigoniaceans of Canada, in which the diverse ornament styles include combinations that blur the distinction between radial and commarginal sculpture.

A comparable problem is encountered in taxa where commarginal ornament is present on part of the flank whereas the other part is smooth. Fleming's (1987: 22) description of the subgenus *Trigonia* (*Heslingtonia*) states that the commarginal costae of the anterior flank stop abruptly near its midline. He noted the similarity of this condition in his New Zealand Triassic material and the Jurassic-Cretaceous Eurasian genus *Psilotrigonia* Cox.

The great diversity of surface sculpture found in post-Paleozoic trigoniaceans encourages the intuitive judgment that the ornament has adaptive significance. This view gains support from experiments by Stanley (1977) and Saul (1978). Stanley concluded that many patterns of trigoniid ornamentation aided burrowing capability. Saul's experiments convinced her that similarities among several Cretaceous groups of knobby trigoniids reflect convergent or parallel adaptations to similar habitats.

These results support Poulton's (1979) opinion that external morphology is evolutionally labile because of its adaptive nature, and thus of lesser taxonomic importance than hinge structure.

REVISION OF OUR 1975 WORK

Given the present state of knowledge of trigoniacean fossils and the need for a classification acceptable to most workers, we conclude that hinge structure should have priority over surface sculpture as a family criterion. In reappraising the classification utilized in our trigoniacean monograph (Newell and Boyd, 1975), we abandon Costatoriidae, return to Cox's (1952) distinction between Myophoriidae and Trigoniidae, demote Eoastartidae to a subfamily of Schizodidae, and retain that family as well as Eoschizodidae, Scaphellinidae, and Pachycardiidae.

In this plan, all genera with trigonian-

grade hinges are grouped in Trigoniidae (Triassic-Recent). Those with myophorian-grade hinges are assigned to either Myophoriidae (Permian-Triassic) or Pachycardiidae (Triassic), depending on size and shape of the major teeth (Newell and Boyd, 1975: 136). The exclusively Paleozoic schizodian-grade hinge characterizes the specialized, monogeneric Schapellinidae (Permian) as well as the diverse Schizodidae (Silurian-Permian). Within the latter family, the Eoastartinae consists of the schizodian-grade members of our former eoastartid group. The one myophorian-grade genus of the Eoastartidae, *Heminajas*, is reassigned to the Pachycardiidae. As we noted in 1975 (p. 136), *Heminajas* shares several characters with other pachycardiids. As for the Eoschizodidae, the taxon continues to exist for one unique Devonian species.

We recognize that our conclusions are strongly influenced by our concentration on pre-Jurassic trigoniaceans. Workers dealing with Jurassic and Cretaceous material are confronted with a bewildering diversity of external morphology produced during the late Mesozoic radiation of the group. Although the typical practice has been to group genera into an expanding array of subfamilies within the Trigoniidae (e.g., Leanza, 1993), a markedly different approach is represented by Cooper's (1991) revision of the order Trigonioida.

His classification recognizes four superfamilies, two of which include more than one hinge grade. These two, Myophoriacea and Trigoniacea, are distinguished by differences in shape, flank/area relationship, and prominence of myophorous buttress. Although most of Cooper's myophoriacean taxa have schizodian hinges and most of the trigoniacean taxa have trigonian hinges, the myophorian hinge is represented in both superfamilies. Cooper's other two superfamilies, Myophorellacea and Megatrigoniacea, are uniformly trigonian in hinge grade. Whereas we follow Cox (1969) and many other workers in accepting the trigonian hinge as the definitive character for the Trigoniidae, Cooper's revision includes nine families with that hinge.

The great diversity of Jurassic and Cretaceous trigonioids may well involve numerous clades that share the trigonian-grade

hinge. Recognition and taxonomic organization of such lineages will require sophisticated methodology. The trigonioids offer great potential for morphometric study and cladistic analysis, and we look forward to the results of such research by workers skilled in those techniques.

NEW SPECIES FROM THE LOWER TRIASSIC OF NEVADA

In the following section, we describe two new trigoniacean species, one smooth (*Neoschizodus*) and the other ornamented (*Lyriomyophoria*), from a silicified fossil assemblage in the Virgin Limestone (Spathian) southwest of Las Vegas. Together with the essentially contemporaneous *Neoschizodus thaynesianus* from the upper Thaynes Formation of northeastern Utah (Newell and Boyd, 1975), they represent the oldest Mesozoic trigoniaceans known to us.

The new species are of particular interest as evidence of the early Mesozoic transition from myophorian to trigonian hinge grades. Furthermore, the ornamented form (*Lyriomyophoria*) represents an intermediate condition between the simple commarginal ornament found in some Paleozoic trigoniaceans and the disparate flank/corselet sculpture typical of post-Triassic members of the superfamily.

The remarkably similar hinges of the two Nevada species exhibit characteristics of both myophorian and trigonian grades. We classify them as myophorian because tooth 2 has the distinctive posterior extension characteristic of that grade. By contrast, they possess the typical, albeit not unique, trigonian feature of a hiatus in the right valve hinge plate. Furthermore, their tooth striation meets the minimum requirement for trigonian grade as defined in a previous section of this report. Both faces of teeth 2 and 3a are consistently striated. This is a notable advance over the situation in *Neoschizodus thaynesianus*, where striation is not only less extensive but also variable within a population (Newell and Boyd, 1975: 144). As in younger trigoniaceans, striae of the two new species are bold, regular, and concave dorsally. However, each ridge has a symmetrical transverse

profile unlike the undercut one typical of advanced trigoniaceans (Cox, 1952: 46).

Although hinges of the two Nevada species are very similar in their mixture of myophorian and trigonian traits, the hinge of the ornamented form is slightly more advanced than that of the smooth form. The former has equally strong striae on both sides of tooth 2 whereas striae are weaker on the posterior side of that tooth in the smooth species. Furthermore, the posterior limb of tooth 2 of the ornamented species is less prominent than its counterpart in the smooth form.

Morphologic terms employed in the taxonomic descriptions that follow are defined either in Cox (1969: 102–109) or in Newell and Boyd (1975: 66–82). Detailed information pertinent to cited locality numbers is in Newell and Boyd (1995: 85–86).

DESCRIPTIONS

FAMILY MYOPHORIIDAE BRONN, 1849

DIAGNOSIS: Small to moderate size shells with prosogyrous to orthogyrous umbones and subangular to rounded posterior ridge. Surface smooth or (less commonly) with commarginal or radial ornament. Myophorian hinge.

DISTRIBUTION: Lower Permian–Upper Triassic.

Genus *Neoschizodus* Giebel, 1855

TYPE SPECIES: *Lyrodon laevigatum* Goldfuss, 1837, SD Stoliczka, 1871; Middle Triassic of Germany.

DIAGNOSIS: Unornamented orthogyrous to moderately prosogyrous shells with slightly incurved beaks. Respiratory margin obliquely truncate and pointed. Posterior ridge angular to subangular in transverse profile. Teeth smooth or incompletely striated.

DISTRIBUTION: Middle and Upper Permian, Kitakami and Gujo formations, Japan; Lower Triassic, upper Thaynes Formation, Utah, and Virgin Limestone, Nevada; Middle Triassic, Muschelkalk Series, Germany.

Neoschizodus elongatus Boyd and Newell, new species

Figure 2

ETYMOLOGY: *elongatus*, from the Latin, long.

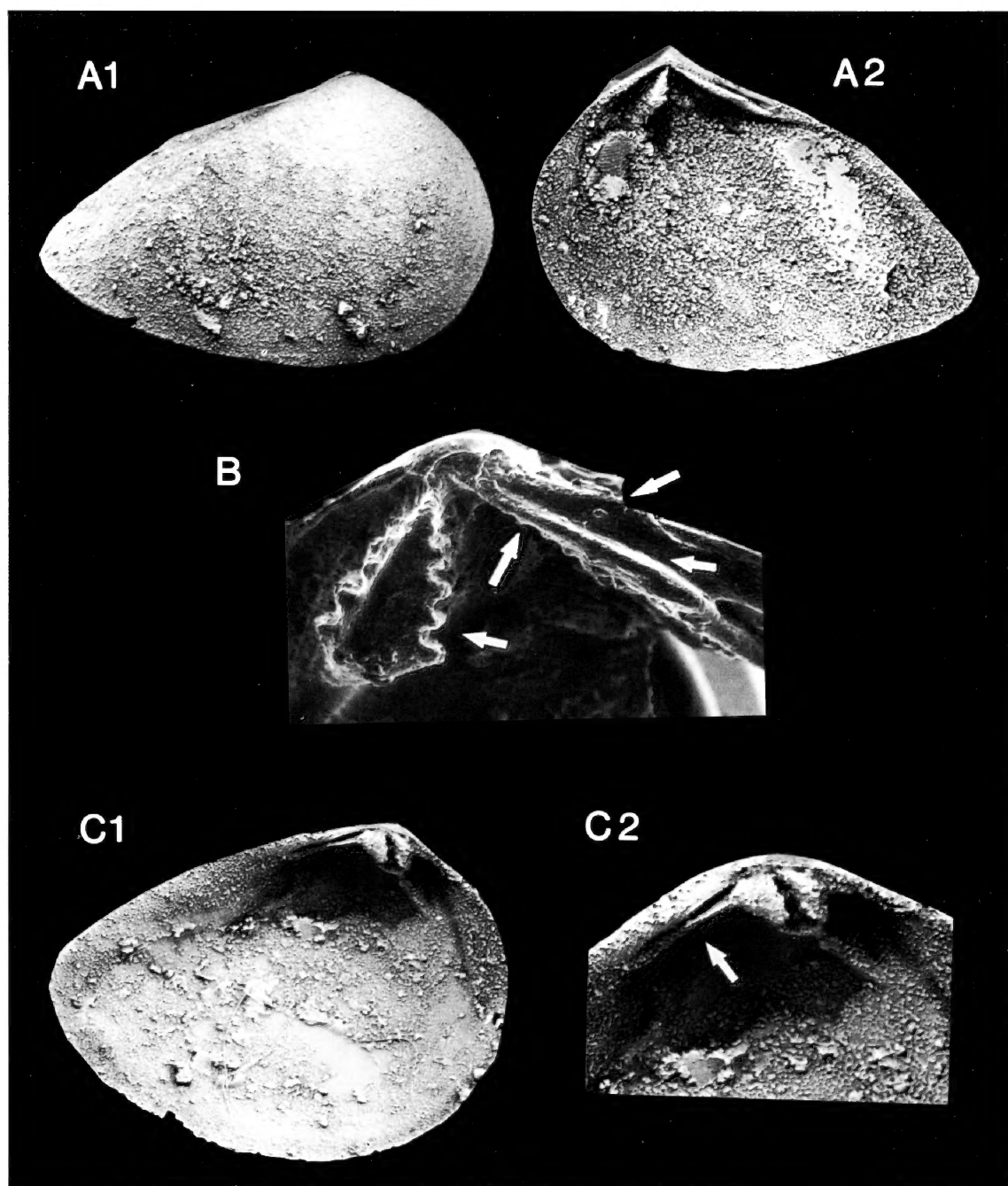


Fig. 2. *Neoschizodus elongatus* Boyd and Newell, n. sp., silicified shells, Lower Triassic, Moenkopi Fm. (Virgin Limestone), Nevada, AMNH loc. B7979. A. Holotype, RV, exterior and interior views each $\times 2$, AMNH cat. 44075; B. RV, $\times 12$, showing deep striae on anterior and posterior faces of tooth 3a (left arrow), weak striae on anterior face of tooth 3b (middle arrow), unstriated socket (right arrow) for reception of tooth 4b, and nymph (upper arrow), SEM stub AMNH cat. 44076; C. LV, $\times 2$ and $\times 3$ respectively, showing posteroventral extension (arrow) of tooth 2 characteristic of myophorian hinge grade, AMNH cat. 44077.

TABLE 1
Neoschizodus elongatus Boyd and Newell, New Species
 AMNH loc. B7979; measurements in millimeters

L	H	L/H	C	H/C	PL ¹	L/PL	T ²	Le ³
Left valves								
31.1	23.3	1.33	7.6	3.07	9.3	3.34	2.5	—
28.4	20.5	1.39	5.6	3.66	8.5	3.34	2.5	3.7
24.4	18.2	1.34	5.2	3.50	8.7	2.80	2.5	—
21.1	16.3	1.29	4.9	3.33	6.7	3.15	—	—
20.7	15.6	1.33	5.0	3.12	6.6	3.14	—	—
15.5	12.2	1.27	3.9	3.13	4.7	3.30	—	—
14.3	10.8	1.32	3.2	3.38	4.7	3.04	1.5	2.1
12.6	9.7	1.30	2.8	3.46	3.8	3.32	1.6	—
11.0	8.2	1.34	2.6	3.15	2.9	3.79	—	—
9.7	8.0	1.21	2.2	3.64	3.7	2.62	—	1.6
Right valves								
33.5	22.7	1.48	7.3	3.11	9.2	3.64	3.4	5.7
29.0	20.3	1.43	6.1	3.33	9.9	2.93	2.9	—
23.7	18.2	1.30	5.6	3.25	7.4	3.20	2.3	3.5
21.6	16.1	1.34	4.5	3.58	6.2	3.48	2.3	—
20.7	16.3	1.27	4.1	3.98	7.3	2.84	2.0	—
18.7	13.5	1.39	3.9	3.46	6.3	2.97	2.0	3.0
16.4	12.9	1.27	3.8	3.39	4.9	3.35	1.9	—
14.5	10.8	1.34	3.4	3.18	4.8	3.02	2.2	—
12.3	9.5	1.29	3.1	3.06	4.1	3.00	—	—
10.2+	8.6	—	2.8	3.07	3.3	—	1.7	2.0

¹ PL = linear extension of valve ahead of beak.

² T = distance from beak to anterior corner of major tooth.

³ Le = length of ligament groove.

DIAGNOSIS: Umbo slightly prosogyrous, beak less than one-third of valve length behind anterior extremity. Anterior and ventral margins form continuous, smooth curve from beak to posterior extremity; respiratory margin broad, gently sloping, meeting dorsal margin with little or no angularity. Posterior ridge angular to carinate initially, becoming broadly rounded beyond valve height of 9 mm. Corselet slightly concave, lacking distinct escutcheon. Small myophorian hinge plate; major tooth on each valve striated on both sides; major socket of right valve unfloored. Anterior adductor scar with dorsal extension for pedal retractor; posterior retractor scar isolated above adductor at end of, respectively, posterior tooth on RV and equivalent socket on LV; pedal elevator scar at apex of umbonal cavity. Pallial line posteriorly truncate, rarely distinct. L/H = 1.34 (n = 39); H/C = 3.30 (n = 26); L/PL = 3.20 (n = 39). L = length; H = height; C = con-

vexity; PL = linear extension of valve anterior to beak.

DISTRIBUTION: Lower Triassic (Spathian) of southern Nevada (Virgin Limestone Member, Moenkopi Formation). AMNH loc. B7977, B7979, B8517.

DISCUSSION: The study collection includes 450 silicified valves from Cottonwood Pass, between Las Vegas and Goodsprings, Nevada. The two collections involved, B7979 and B8517, are thought to be from the same stratum, offset by a fault. All valves are disarticulated, many are broken, and most have the interior concealed by a coarse silica crust and/or silicified matrix. Although most exteriors are well preserved, examination of many outer surfaces provided no evidence of original microstructure. The same species is represented by more than 150 internal molds in our collection from loc. B7979 east of Las Vegas. Here, silica coated the inner surface

of the valve and replaced adjacent matrix, but the shell was not silicified.

Although most shells of *N. elongatus* are unornamented, rare valves exhibit indistinct commarginal ridges on the anterior slope. The ligament groove length is about equal to that of the right-valve posterior tooth. A posterior tooth is weakly developed on large left valves but is unrecognizable on small valves. The corresponding socket on large right valves is an unstriated furrow separating a slender posterior tooth from the narrow nymph.

The new species is distinguished from the approximately coeval *Neoschizodus thayneianus* by its more elongate form, less angular posterior margin, smaller hinge plate, and more thoroughly striated teeth. In the last-mentioned character, *N. elongatus* differs from the minimal trigonian condition only in the inequality between striae of the two sides of tooth 2. In all but the largest left valves, the posterior face of that tooth is only weakly striated.

Genus *Lyriomyophoria* Kobayashi, 1954

TYPE SPECIES: *Lyriodon elegans* Dunker, 1849, OD; Middle Triassic of Germany.

DIAGNOSIS: Prosogyrous shells with subdued umbones; truncate respiratory margin greater than half valve height. Posterior ridge sharply defined. Prominent commarginal ridges on both corselet and flank; corselet interrupted by radial groove. Myophorian hinge with striae on some teeth.

DISTRIBUTION: Triassic; Eurasia, North Africa, Nevada.

Lyriomyophoria paullorum Boyd and Newell, new species

Figures 3, 4

ETYMOLOGY: *paullorum*, for Drs. Rachel and Richard Paull, experts on Lower Triassic stratigraphy of the Rocky Mountains and Great Basin.

DIAGNOSIS: Slightly prosogyrous shells with height nearly equal to length; beaks slightly forward of midlength. Anterior margin strongly convex; respiratory margin high and rectilinear, meeting dorsal margin at obtuse angle. Posterior ridge marked by prominent carina but without adjacent trough.

Commarginal ridges in front of posterior ridge larger and more regular in form and spacing than those of corselet; escutcheon narrow and inconspicuous. Myophorian hinge with prominent striae on both sides of the major tooth on each valve; major socket of right valve unfloored. $L/H = 1.08$ ($n = 20$); $H/C = 3.66$ ($n = 20$); $L/PL = 2.57$ ($n = 20$).

DISTRIBUTION: Virgin Limestone Member (Spathian), Moenkopi Formation, near Las Vegas, Nevada. AMNH loc. B7977, B7979, B8517.

DISCUSSION: *Lyriomyophoria paullorum* occurs with the smooth trigoniacean *Neoschizodus elongatus* in our samples of Virgin Limestone from the Las Vegas area. Our study collection consists of several hundred disarticulated valves, most of them fragmental and imperfectly silicified. The RV/LV ratio is approximately 3/2. Fewer well-preserved interiors are present than in the *N. elongatus* collection, but the number and position of muscle scars appear to be the same in both species.

The prominent commarginal ridges in front of the posterior ridge are narrower than the valleys between them, in contrast to the finer, more numerous ones of the corselet where discontinuous and anastomosing ridges are common. The corselet is divided into anterior and posterior parts by an arcuate groove, most prominent as a midline in the markedly concave dorsal part of the corselet. A diminutive escutcheon is bordered by a threadlike carina. On one well-preserved valve, 11.6 mm long, the escutcheon extends 4.3 mm behind the beak and is 0.7 mm in maximum width.

The myophorian hinge is close to the trigonian grade in that both sides of the major tooth in each valve are thoroughly striated, the posterior limb of the left-valve major tooth is short, and a hiatus is present in the right-valve hinge plate. The left-valve major tooth is relatively narrow; its two sides diverge at an average angle of 51° ($n = 6$). The notably short ligament groove is about half the length of the right-valve posterior tooth.

L. paullorum differs from the type species of the genus in that commarginal ridges do not cross the carina on the posterior ridge, and there is no trough bordering the ridge.

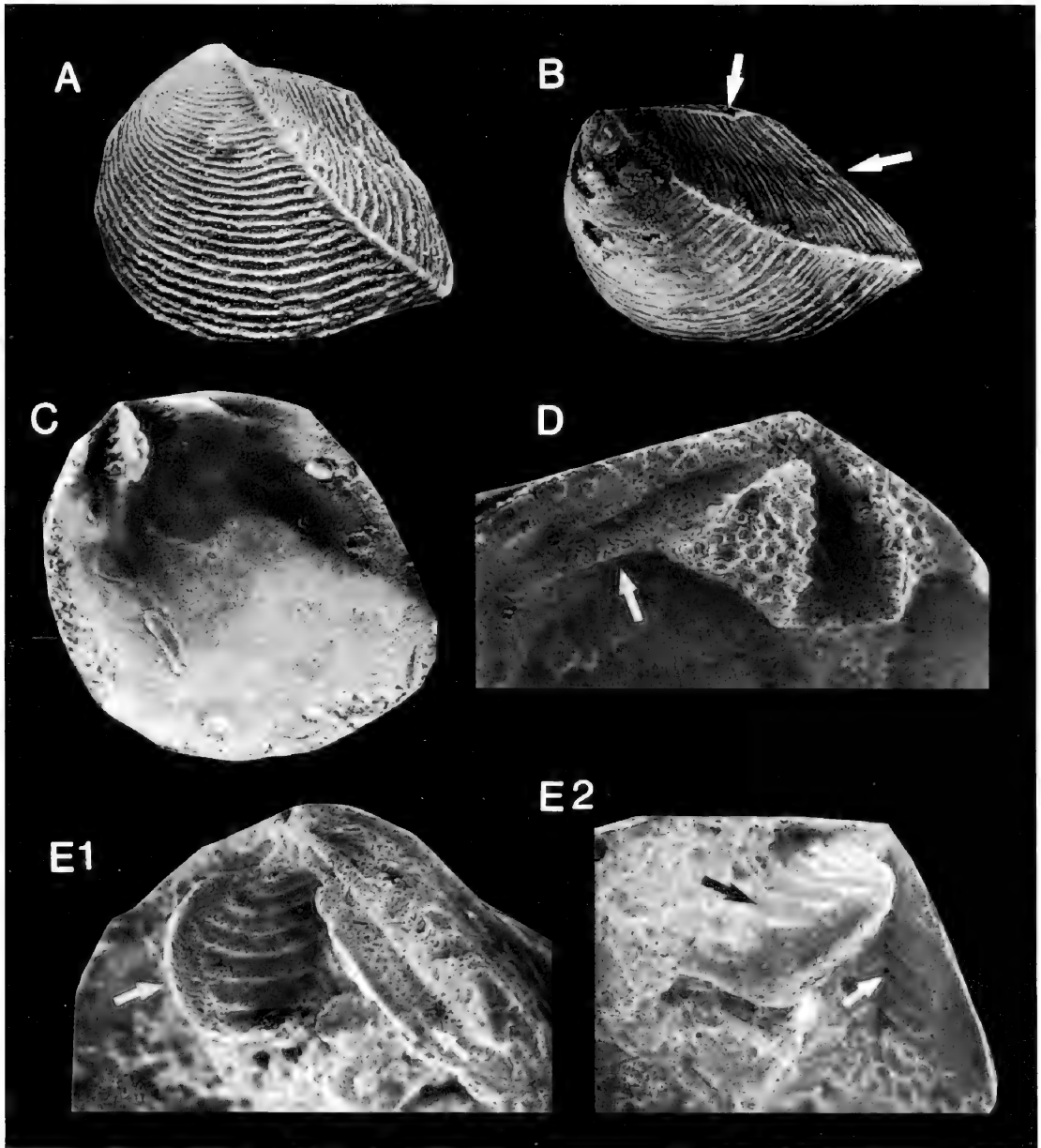


Fig. 3. *Lyriomyophoria paullorum* Boyd and Newell, n. sp., silicified shells, Moenkopi Fm. (Virgin Limestone), Nevada. **A.** Holotype, LV, $\times 3$, showing carinate ridge not crossed by commarginal ornament, AMNH loc. B8517, cat. 44078; **B.** LV, $\times 3$, posterodorsal view showing contrast between ornament on both sides of carina, narrow escutcheon (upper arrow), and shallow furrow (lower arrow) bisecting corselet, AMNH loc. B8517, cat. 44079; **C.** RV, $\times 3$, AMNH loc. B8517, AMNH cat. 44081; **D.** LV, $\times 12$, showing posteroventral wing (arrow) of tooth 2. Pitted surface and lack of striae are effects of imperfect fossilization, AMNH loc. B8517, SEM stub AMNH cat. 44080; **E.** RV, $\times 12$, AMNH loc. B7979, SEM stub AMNH cat. 44082; **E1.** downward convex striae on posterior face of tooth 3a (left arrow) and nonstriated socket (right arrow) for reception of tooth 4b; **E2.** same specimen tilted to expose striated anterior faces of tooth 3a (left arrow) and tooth 3b (right arrow).

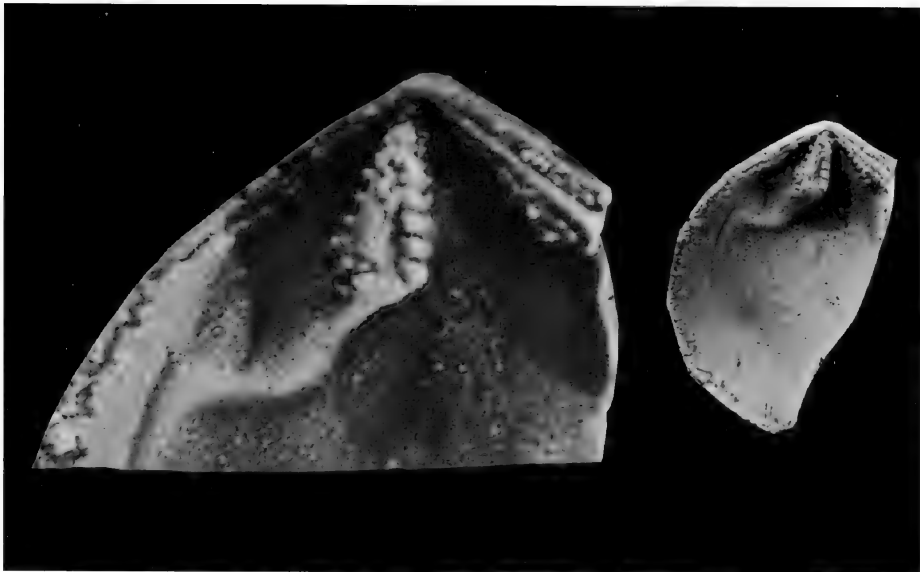


Fig. 4. *Lyriomyophoria paullorum* Boyd and Newell, n. sp., RV, $\times 9$ and $\times 3$, shows myophorous buttress supporting major tooth 3a, bordering ventral side of anterior adductor scar, AMNH loc. B8517, AMNH cat. 44083.

TABLE 2
Lyriomyophoria paullorum Boyd and Newell, New Species
AMNH loc. B7979; measurements in millimeters

L	H	L/H	C	H/C	PL ¹	L/PL	T ²
Left valves							
14.2	13.2	1.08	3.7	3.57	5.7	2.49	2.8
13.6	12.9	1.05	3.2	4.03	5.6	2.43	2.5
13.2	12.2	1.08	3.2	3.81	4.2	3.14	2.3
12.8	12.0	1.07	3.3	3.64	5.4	2.37	2.3
11.1	10.5	1.06	2.8	3.75	5.0	2.22	2.0
10.8	10.4	1.04	2.8	3.71	4.3	2.51	2.0
10.5	9.8	1.07	2.8	3.50	3.9	2.69	1.9
10.3	9.1	1.13	2.7	3.37	3.9	2.64	2.1
9.4	8.8	1.07	2.4	3.67	3.8	2.47	1.6
9.4	8.9	1.06	2.2	4.05	4.0	2.35	1.6
Right valves							
14.1	13.6	1.04	3.8	3.58	5.6	2.52	3.0
13.8	11.5	1.20	3.0	3.83	5.1	2.71	2.9
13.2	11.5	1.15	3.3	3.48	4.7	2.81	2.5
12.6	11.2	1.13	2.9	3.86	5.0	2.52	2.3
12.4	11.5	1.08	3.2	3.59	4.5	2.76	2.4
11.1	11.1	1.00	3.0	3.70	5.0	2.22	2.2
11.0	10.8	1.02	3.1	3.48	4.4	2.50	2.3
10.3	9.8	1.05	2.6	3.77	3.6	2.86	2.1
10.1	8.9	1.13	2.5	3.56	4.1	2.46	1.9
8.1	7.6	1.07	2.3	3.30	3.0	2.70	—

¹ PL = linear extension of valve ahead of beak.
² T = distance from beak to anterior corner of major tooth.

Furthermore, the new species has a very short ligament groove and prominently striated major teeth.

In overall valve shape and in the disparate condition of commarginal ornament between flank and corselet, *L. paullorum* resembles the Permian schizodian-grade *Lyroschizodus orbicularis*. The latter species lacks myophorous buttresses and carinate posterior ridge.

Similar inequality of commarginal ornament between flank and corselet characterizes the Upper Triassic *Prosogyrotrigonia* and the Jurassic-Cretaceous *Trigonia* (*Frenquelliella*). The former lacks a posterior carina and a truncate respiratory margin. The latter is opisthogyrous and its corselet ridges originate in a sulcus in front of the posterior ridge.

ACKNOWLEDGMENTS

The new species described here were discovered during fieldwork supported by National Science Foundation grants EMS 74-12372, DEB 77-01558, and BSR 88-06186.

Drs. Knut Andersson and Xunhong Chen, then graduate students at the University of Wyoming, provided excellent field assistance, and Chen did much of the laboratory acid processing of the limestone. Gillian Newell participated fully in the fieldwork and in production of the final manuscript. Walter Elvers has volunteered his services in the organization of the collections, and has assisted enthusiastically in many other ways.

Our respective institutions, the University of Wyoming and the American Museum of Natural History, provided office, laboratory, and other facilities. Scanning electron microscopy was done at the University of Wyoming by Keith Krugh. Andrew Simon and Portia Rollings, under Newell's guidance, did the photography at the American Museum of Natural History.

Although not every suggestion from reviewers Terrence Poulton, Steven Stanley, and Thomas Waller was followed, the paper is much better as a result of their work, and we thank them for their efforts.

REFERENCES

- Boyd, D. W., and N. D. Newell
1968. Hinge grades in the evolution of cras-satellacean bivalves as revealed by Permian genera. *Am. Mus. Novitates* 2328: 52 pp.
- Cooper, M. R.
1991. Lower Cretaceous Trigonioida (Mollusca, Bivalvia) from the Algoa Basin, with a revised classification of the order. *Ann. S. African Mus.* 100(1): 52 pp.
- Cox, L. R.
1952. Notes on the Trigoniidae with outlines of a classification of the family. *Proc. Malacol. Soc. London* 29: 45-70.
1969. Superfamily Trigoniacea, Family Myophoriidae Bronn, 1849 and Family Trigoniidae Lamarck, 1819. In R. C. Moore (ed.), *Treatise on invertebrate paleontology* N(1), Mollusca 6: 471-488. Lawrence: Geol. Soc. Am. and Kansas Univ.
- Farsan, N. M.
1972. Stratigraphische und paläogeographische Stellung der Khenjan-Serie und deren Pelecypoden (Trias, Afghani-stan). *Palaeontogr., Abt. A.*, 140: 131-191.
- Fleming, C. A.
1963. A new genus and species of Trigoniidae from the Middle Triassic of New Zealand. *New Zealand J. Geol. Geophys.* 6(5): 843-846.
1964. History of the bivalve family Trigoniidae in the south-west Pacific. *Australian J. Sci.* 26(7): 196-204.
1987. New Zealand Mesozoic bivalves of the Superfamily Trigoniacea. *New Zealand Geol. Surv. Paleontol. Bull.* 53: 74 pp.
- Harrison, W. B. III, and L. K. Harrison
1975. A Maquoketa-like molluscan community in the Brassfield Formation (Early Silurian) of Adams County, Ohio. *Bull. Am. Paleontol.* 67: 193-234.
- Ichikawa, K.
1954. Late Triassic Pelecypods from the Kouchigatani Group in the Sakurandani and Kito areas, Tokushima Prefecture. Shikoku, Japan, part 11. *J. Inst. Polytech, Osaka City Univ., Ser. G*, 2: 53-72.
- Johnston, P. A.
1993. Lower Devonian Pelecypoda from

- southeastern Australia. Assoc. Australasian Palaeontol. Mem. 14: 134 pp.
- Kobayashi, T.
1954. Studies on the Jurassic Trigonians in Japan, part 1. Preliminary notes. Japanese J. Geol. Geogr. 25(1-2): 61-80.
- Leanza, H. A.
1993. Jurassic and Cretaceous bivalves from west-central Argentina. Bull. Am. Paleontol. 105(343): 95 pp.
- Newell, N. D., and D. W. Boyd
1975. Parallel evolution in early trigoniacean bivalves. Bull. Am. Mus. Nat. Hist. 154(2): 162 pp.
1995. Pectinoid bivalves of the Permian-Triassic crisis. Ibid. 227: 95 pp.
- Pojeta, J. Jr., R. Zhang, and Z. Yang
1986. Chapter G. Systematic paleontology of Devonian pelecypods of Guangxi and Michigan. In J. Pojeta, Jr. (ed.), Devonian rocks and Lower and Middle Devonian pelecypods of Guangxi, China, and the Traverse Group of Michigan. U.S. Geol. Surv. Prof. Pap. 1394-A-G: 57-107.
- Poulton, T. P.
1979. Jurassic trigoniid bivalves from Canada and western United States of America. Geol. Surv. Can. Bull. 282: 82 pp.
- Saul, L. R.
1978. The North Pacific Cretaceous trigoniid genus *Yaadia*. Univ. California Publ. Geol. Sci. 119: 65 pp.
- Stanley, S. M.
1977. Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. Palaeontology 20(4): 869-899.
1978. Aspects of the adaptive morphology and evolution of the Trigoniidae. Philos. Trans. R. Soc. London B(284): 247-258.
- Waller, T. R.
1981. Functional morphology and development of veliger larvae of the European oyster, *Ostrea edulis* Linné. Smithsonian Contrib. Zool. 328: 70 pp.

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